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A SORICID AND TWO ERINACEIDS FROM THE
WHITE RIVER OLIGOCENE

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The study presented in the following pages is due to a fortunate coincidence of collecting. For several years past, one of us (P. O. McG.) has been working certain lower Brulé exposures in north-western Nebraska for small mammals. Field Museum recently received from Mr. James Mellinger of Longmont, Colorado, a representative sample of the microfauna found in a lower Brulé channel deposit in northeastern Colorado. Each of these two collections contained good specimens of new or little-known insectivores, the material from one locality supplementing that from the other in a most gratifying way. Study of these specimens has established two genera known hitherto from very incomplete material, and has made possible certain interesting taxonomic reassignments.

We wish to express our sincere thanks to the Staff of the Department of Vertebrate Paleontology of the American Museum for their many kindnesses during our visits there, and particularly to Dr. Walter Granger for permitting us to borrow and redescribe the holotype of *Domnina gradata* Cope. We are indebted to Mr. James Mellinger for his gift of specimens to Field Museum. Mr. Michael S. Chappars of Walker Museum kindly permitted the use of his Leica camera for taking the photomicrographs. Most of the Nebraska specimens were collected by Winifred Cook McGrew. Some rodent specimens from Mr. Mellinger's locality have been examined by Dr. Albert Elmer Wood. He has kindly informed us that they indicate lower Brulé age.

The technique employed in making the accompanying photomicrographs will be described elsewhere by McGrew.

Soricidae Gray

Domnina Cope

Domnina Cope 1873, Pal. Bull., No. 16, p. 1.

Protosorex Scott 1894, Proc. Acad. Nat. Sci. Phila., p. 446.

Genotype.—*Domnina gradata* Cope 1873.

Distribution.—Middle Oligocene, Lower Brulé beds, Colorado, South Dakota, Nebraska.

Emended diagnosis.— I_1^3 , C_0^0 , P_4^3 , M_3^3 . Teeth heavily pigmented. P^2 lacking. P^4 with small protocone and hypocone. Upper molars with hypocones resembling those of *Blarina*; posterior cingula extending externally to metastyles. I_3 less procumbent than in recent genera, without accessory cuspules, alveolar rim not extending posteriorly beneath premolars. P_{1-3} small; P_1 larger than P_{2-3} ; P_4 the largest of the series with single, conical, anteriorly projecting cusp, and relatively strong transverse posterior cingulum. Lower molars progressively reduced in size from M_1 to M_3 , protoconids and hypoconids sharply angulate externally, strong antero-external cingula; entoconids of M_{1-3} high, and connected by ridges to posterior slopes of metaconids. Talonid of M_3 reduced, hypoconid small, entoconid greatly reduced or absent. Horizontal ramus heavy, deep, straight beneath molars, mental foramen beneath M_1 .

Remarks.—This interesting genus has had a peculiarly checkered taxonomic history—a somewhat surprising fact—for when proper comparisons are made, the fundamental resemblances of the lower molars of the holotype to those of the soricids are at once apparent. In his type description, Cope (1873a, p. 1) made no statement as to affinities. Subsequently (1874, p. 465) he stated that "*Domnina* Cope, and probably *Embassis* Cope [= *Peratherium*], present affinities to the Soricidae, so far as known," but in 1884 (pp. 788, 810) he changed his earlier view and referred the animal, with some doubt, to the Chiroptera. This assignment was followed without comment by several early workers. Zittel (1893, p. 562) placed *Domnina* in the Ictopsidae (= Leptictidae), and in this he was followed by Hay in his first bibliography. Matthew at first (1899, p. 55) referred to it as "Insectivora inc. sed.," and later (1909a, p. 105) placed it in the Talpidae. Haug (1922, p. 1528) went so far afield as to include it in his Oligocene faunal list as a rodent. In recent years the consensus has been that it is a member of the Talpidae (Hay, second bibliography, Cook and Cook 1933, Scott and Jepsen 1936).

The type of *Protosorex crassus* Scott was formerly in Walker Museum, but is now unfortunately lost. The specimens collected by Mellinger and McGrew in Colorado and Nebraska agree with the description of this form, and also with the holotype of *Domnina*, thus leaving no doubt that *Protosorex* must be relegated to synonymy.

Scott made no mention of pigment on the teeth. The holotype of *Domnina gradata* appeared to show no pigment, whereas our material is richly pigmented. There appeared to be a possibility, therefore, that the new specimens might represent a distinct genus distinguished from the two previously described specimens by the presence of pigment. To test this possibility the holotype of *D. gradata*, the referred specimens, and a specimen each of *Blarina brevicauda* and of *Peratherium* sp. (collected in the locality at which part of the referred material of *Domnina* was found) were examined under ultra-violet light. Under this light the pigmented portions of the enamel of *Blarina* did not fluoresce, in sharp contrast to the unpigmented areas which fluoresced a bluish violet color. The enamel of *Peratherium* fluoresced a yellowish white color, uniform on all parts. Our specimens of *Domnina*, on which the pigmentation is very apparent in ordinary light (see figs. 61, 62, 64), fluoresced dull orange on the pigmented areas and yellowish white, as in the *Peratherium* specimen, on the unpigmented. The holotype was then examined with results identical to those obtained for the referred specimens. From this evidence, and in the absence of the holotype of *P. crassus*, it is legitimate to assume that the specimen described as *Protosorex* was pigmented also. The heavily pigmented teeth of *Domnina* indicate that colored enamel was acquired early in the history of Soricidae. In view of the interesting results obtained from this material by the use of ultra-violet light, it would seem desirable to examine all fossil soricids in a similar manner.

The dental formula followed is that proposed by Ärnabäch-Christie-Linde (1912), and employed by Cabrera in his catalogue of the recent insectivores (1925).¹ The teeth immediately following the upper and lower incisors have been regarded by most authors as canines. In a study of the development of the anterior teeth in *Sorex*, Ärnabäch found, however, that in embryos there were present the germs of five upper and four lower incisors, an upper and lower canine, and four upper and lower premolars. Of these only the last three upper and the last lower incisors, the upper premolars, and P₁

¹ This able and useful work, and its companion volume on the recent marsupials, does not appear to be as widely known among paleontologists as it deserves.

and P_1 persisted, the rest disappearing before birth. A vestigial milk dentition was also observed. Similar results, save for some details, were obtained for *Neomys*. *Domnina*, in which the lower premolars are all present and P_1 and P_2 larger than P_{2-3} , provides some support for Ärnäsch's views, as noted by her (1912, p. 623). Discovery of still earlier soricids should provide further tests of this formula.

Domnina gradata Cope (figs. 60–65)

D. gradata Cope 1873, Pal. Bull., No. 16, p. 1.

Miothen crassigenis Cope 1873, Synopsis Vertebrata Colorado, p. 8; *D. crassigenis* Cope 1874, Ann. Rept. U. S. Geol. Geog. Surv. Terr., 1873, p. 470.

Protosorex crassus Scott 1894, Proc. Acad. Nat. Sci. Phila., p. 446.

Holotype.—Amer. Mus. No. 5353. Portion of right horizontal ramus with M_{1-3} .

Horizon and locality of holotype.—Lower Brulé beds, Cedar Creek, Logan County, Colorado.

Referred specimens.—F.M. No. P15320, incomplete left mandible with I_3 , P_4 , M_{1-3} , alveoli of P_{1-3} ; collected in the lower Brulé beds, Sec. 12, R. 65 W., T. 11 N., three miles northwest of Gault Schoolhouse, Weld County, Colorado, by Mr. James Mellinger. Univ. Chicago No. 1547, portion of right ramus with M_{1-3} ; Univ. Chicago No. 1550, portion of left ramus with M_2 ; Univ. Chicago No. 1551, portion of left maxillary with M^{1-2} ; all collected by McGrew in the lower Brulé beds, twelve miles north-northwest of Crawford, Dawes County, Nebraska. Univ. Chicago No. 1552, portion of left ramus with M_{1-3} and alveoli of P_{1-4} ; Univ. Chicago No. 1553, portion of left ramus with M_{1-3} and alveoli of P_{1-4} ; both collected by McGrew in the lower Brulé beds ten miles northeast of Harrison, Sioux County, Nebraska. Univ. Chicago No. 1554, incomplete facial region with left P^2 , lingual portion of P^4 , and alveoli of I^{1-3} , P^1 ; collected by McGrew in the lower Brulé beds two and one-half miles north of Chadron, Dawes County, Nebraska.

Diagnosis.—As for the genus; for measurements see p. 256.

Remarks.—The description and measurements given by Scott for *P. crassus* indicate that this species must be placed in the synonymy of *D. gradata*. The holotype of *D. crassigenis* (Cope) consists of a pair of incomplete mandibles with heavily worn lower molars. The specimen shows no characters that might serve to separate it from *D. gradata*. Cope's "*Miothen*" *gracile* (1873b, p. 8), referred to *Domnina* in 1874 (p. 470), was later regarded by him (1884, p. 796) as a synonym of *Peratherium huntii* (Cope).

Description.—The incomplete facial region shows the alveoli of the large I^1 , the small I^{2-3} , and the small P^1 . P^2 is much larger than P^1 , and consists of a single anteriorly placed cusp. External, internal, and posterior cingula are present; a low, rather sharp crest runs posteriorly from the apex of the cusp to the posterior cingulum.



FIG. 60. *Domnina gradata* Cope. Univ. Chicago No. 1551. Left M^{1-2} in maxilla fragment; external, crown, and internal views. $\times 5$

P^3 is lacking. This tooth is greatly reduced in some modern genera, and absent in others. The lingual portion only of P^4 is preserved. The protocone and hypocone are not well differentiated, and appear as anterior and posterior swellings on an internal ridge.

M^{1-2} are very similar to corresponding teeth of *Blarina*, the only observable difference being that the strong posterior cingulum extends externally to a point immediately posterior to the metastyle.

The other existing forms differ in having the posterior border of the molars indented.

I_3 is strikingly different from that of other soricids. It is large and only moderately procumbent, forming an angle of about 30° with the ventral border of the ramus. The tip is broken off; the remaining part shows a very slight upward curve. The tooth is roughly oval in cross-section, the dorso-ventral diameter being greater than the transverse. The alveolus is anterior to that of P_1 ,



FIG. 61. *Domnina gradata* Cope. F. M. No. P15320, incomplete left mandible with I_3 , P_4 - M_3 ; crown view. $\times 5$

and the ventral border of the tooth therefore does not extend back beneath the premolars—a decided contrast to the living forms. No accessory cusps are present, their places being taken by a low but sharp crest on the labial side of the dorsal face, at the base of which is a slight groove for the overlapping P_1 . The outer side of the crown is heavily pigmented.

The presence of P_{2-3} distinguishes *Domnina* from all other known shrews, living and fossil. The alveoli of these teeth are considerably smaller than those of P_1 and P_4 . The teeth themselves were in all probability greatly reduced. P_4 is slender and high. It is composed of a triangular cusp with its apex extending anteriorly, and a low

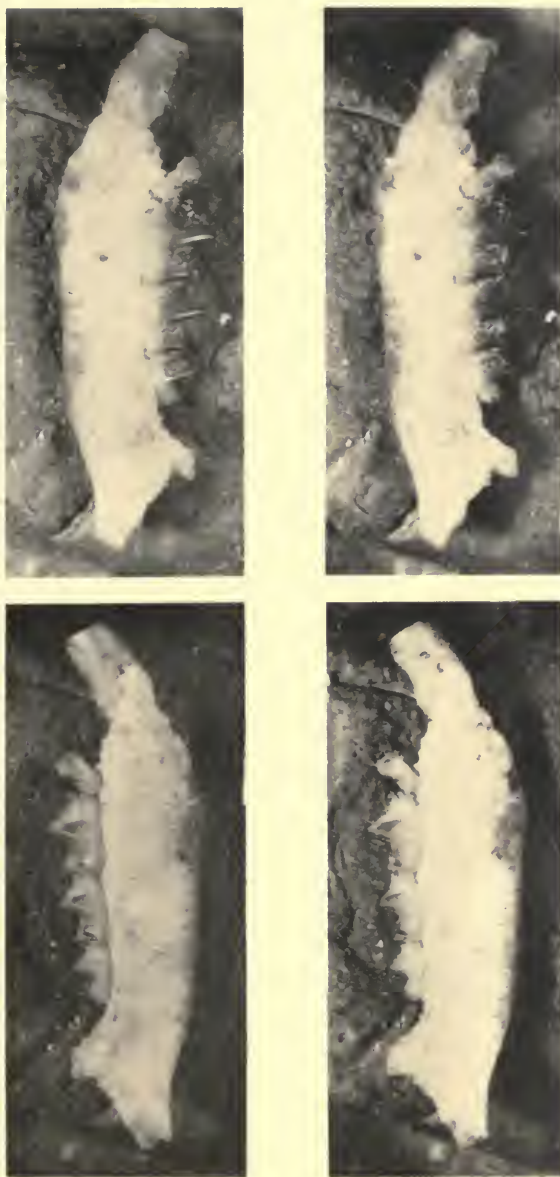


FIG. 62. *Domnina gradata* Cope. F. M. No. P15320, incomplete left mandible with I_3 , P_4 - M_3 ; external and internal views. $\times 5$

broad cingulum heel. Slight external and internal cingula are present. The cusp extends well forward over the alveolus of P_3 .

The heavily pigmented molars decrease in size posteriorly. The trigonids are longer and higher than the talonids. The paraconid is a large, well separated cusp connected by a low ridge to the anterior

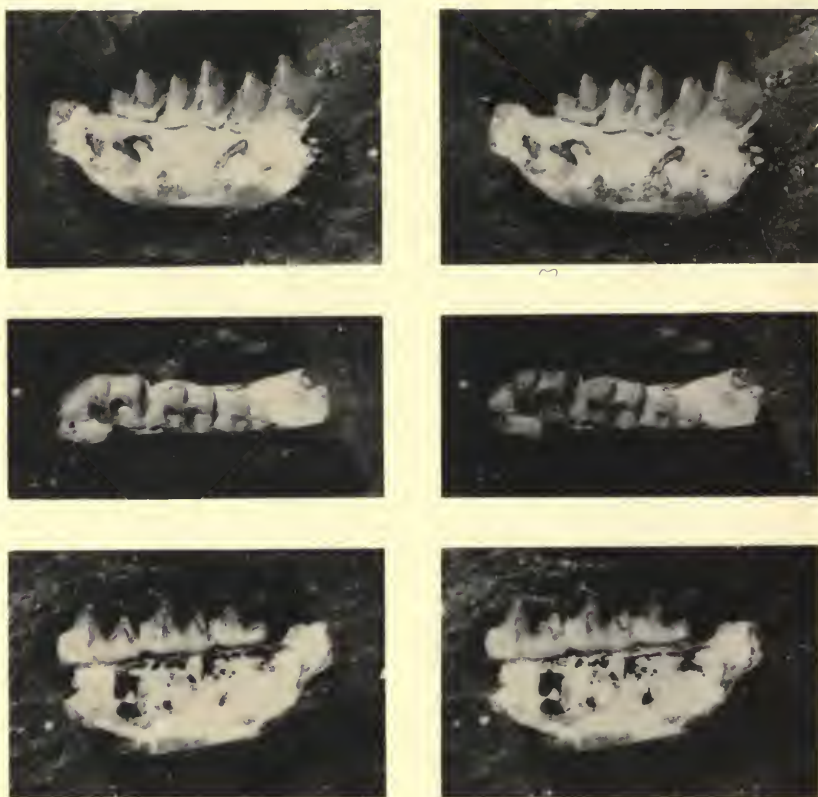


FIG. 63. *Domnina gradata* Cope. Amer. Mus. No. 5353. Holotype. Portion of right ramus with right M_{1-3} ; external, crown, and internal views. $\times 5$

slope of the protoconid. The metaconid is directly lingual to the protoconid. The latter cusp is sharply angulate externally. A prominent antero-external cingulum is present. An external cingulum is present on the hypoconid. The anterior slope of the hypoconid extends downward and forward to the protoconid-metaconid crest, its internal slope (possibly including the hypoconulid)

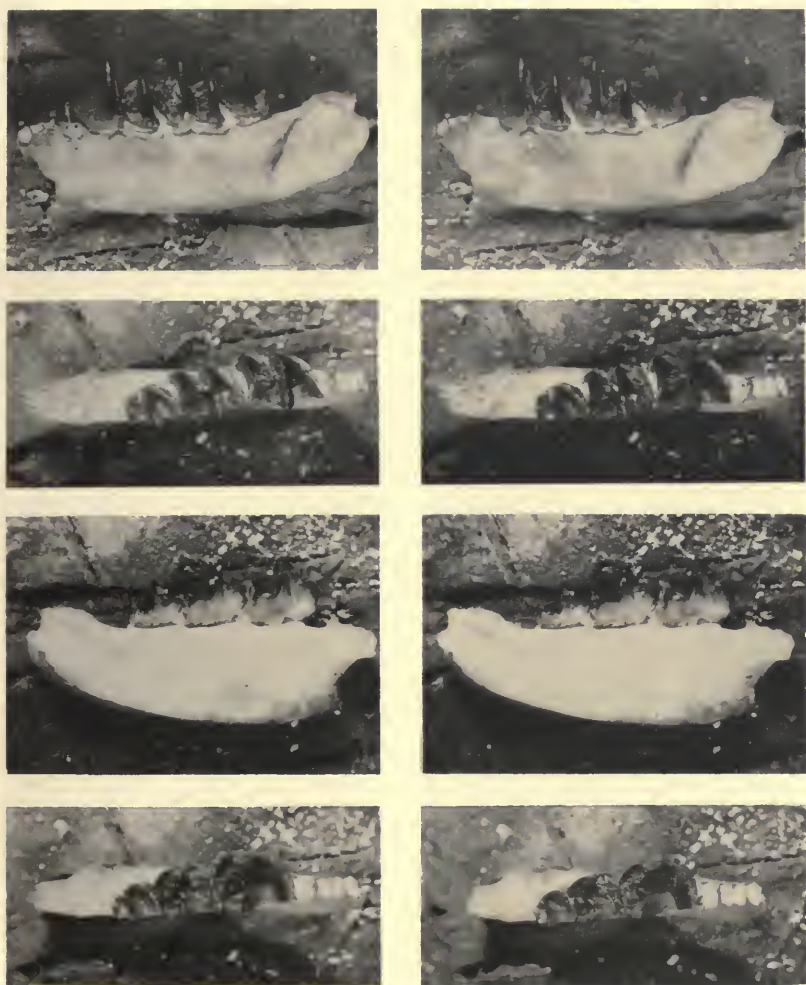


FIG. 64. *Domnina gradata* Cope. Univ. Chicago No. 1552. Portion of left mandible with M_{T-3} ; external, crown, and internal views, crown view with specimen tipped to show the premolar alveoli. $\times 5$

extends inward behind the entoconid to the lingual margin of the tooth.¹ The entoconid of M_{T-2} is a large, transversely compressed cusp, which is not united to the posterior wall of the tooth. It is connected by a sloping ridge to the posterior face of the metaconid, thus forming a lingual wall to the talonid basin. On M_T the

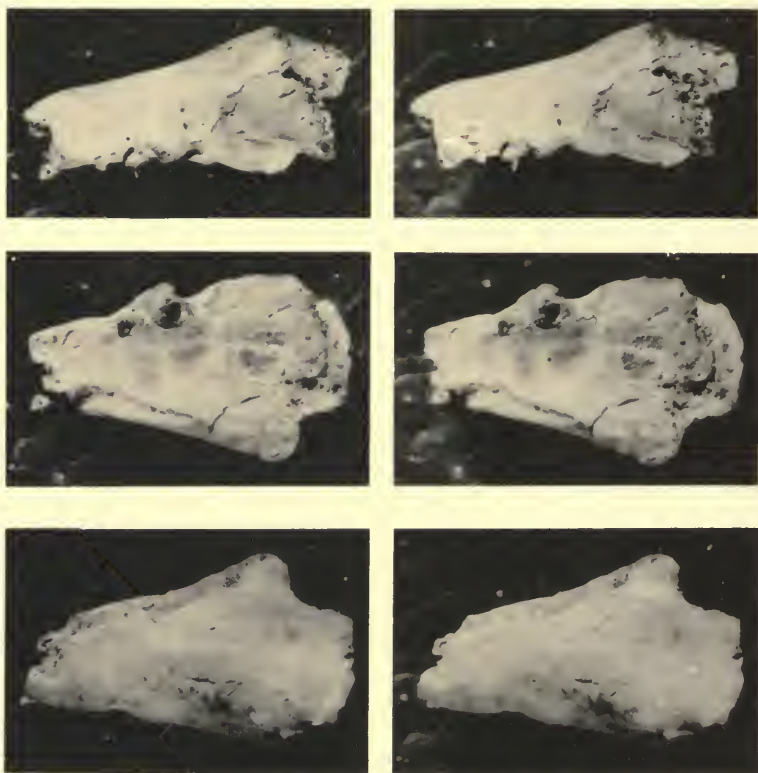


FIG. 65. *Domina gradata* Cope. Univ. Chicago No. 1554. Incomplete facial region with left P^2 , lingual portion of P^3 ; lateral, ventral, and dorsal views. $\times 4$

talonid is wider than the trigonid, on M_2 trigonid and talonid are about equal in width, and on M_3 the talonid is greatly reduced.

¹ We believe that the cusp regarded by Stirton (1930, fig. 1) as the entoconulid on the molars of *Limnoecus* is the entoconid, and that the rather slight projection immediately posterior to it is either the hypoconulid or merely a projection of the ridge which runs lingually from the hypoconid. An apparent inconsistency may also be noted in this paper. The well developed postero-internal cusp in M_T and M_2 of *Crocidura russula russula* is labeled "end" on Fig. 2, whereas on p. 220 the following statement appears: "In the *Crocidura* group the entoconid is absent, and the entoconulid is well developed on M_{T-2} ."

The entoconid is either absent on M_3 (F.M. No. P15320), or reduced to a low, inconspicuous ridge (Univ. Chicago No. 1552).

The skull fragment adds nothing to the description already given by Scott. The rostrum is relatively wider than in most of the recent shrews examined, but is approximately equalled in this respect by *Nectogale*. The mandible has a strikingly deep horizontal ramus. The ventral border is straight beneath the molars, but turns upward at an angle of about 30° beneath the premolars. The alveolar border is nearly horizontal from M_3 forward to P_4 , turning downward toward the incisor under the anterior premolars. On the inner face of the ascending ramus of F.M. No. P15320 there is a small rounded notch above which the jaw is broken away; this may be the ventral border of an intertemporal fossa. This notch is situated below a line projected back from the cusps of the molars and is just slightly above a line projected along the alveolar border. It is possible that this apparent border is an angular break which has been rounded by the erosional action of water. In *Heterosorex*, a primitive form sharing several characters with *Domnina*, the intertemporal fossa is absent, a fact which might argue for absence in *Domnina*. More complete material will be necessary before the presence or absence of the fossa in *Domnina* can be proved definitely. The holotype of "*P. crassus*" lacked the condyle and angle; Scott made no mention of the fossa, the specimen presumably being broken in this region also.

Relationships.—It is not possible at present to arrive at a satisfactory conclusion regarding the position of *Domnina* in soricid phylogeny. The genus is primitive (for the Soricidae), and as such might be regarded as structurally ancestral to many of the living forms. That it is actually ancestral to any of them seems doubtful. The occurrence of Miocene species referred to living genera (See the catalogue of fossil shrews given by Stirton 1930, pp. 220–223.) would appear to indicate that the differentiation of the family into the groups now surviving may have taken place as early as the Oligocene, if not earlier.

Domnina and the Miocene genus *Heterosorex* (Gaillard 1915) have several characters in common, as stated above. The molar patterns and proportions of the two genera are very similar, and the horizontal rami of both are deep and heavy, and of comparable proportions. *Heterosorex*, however, retains part of the zygomatic arch, a structure already lost in *Domnina* (Scott 1894, p. 446). The antemolar dentition of *Heterosorex* is, on the other hand, much more specialized than that of *Domnina*. There are but two upper and

lower premolars, and P_T is much larger than P_4 . The two forms may be members of a group of related genera, or the resemblances between them may indicate nothing more than a common retention of certain heritage characters. Among living genera, *Blarina* closely approaches *Domnina* and *Heterosorex* in upper and lower molar structure. Stirton (1930, p. 219) considers *Heterosorex* to be more closely related to the "Blarinae" than to other living shrews. This may be the case, but it will require much more fossil material than is now available before any satisfactory phylogenetic arrangement of the family can be made.

MEASUREMENTS IN MILLIMETERS

	U. C. 1554	U. C. 1551	Holotype A. M. 5353	P15320	U. C. 1549	U. C. 1552	U. C. 1547 "P. crassus"*
P_2^a , a.-p.	1.0
P_2^a , tr.	0.9
M_1^1 , a.-p.	1.9
M_1^1 , tr.	2.0
M_2^2 , a.-p.	1.7
M_2^2 , tr.	2.0
Length, P_T - M_3	7.0
P_4 , a.-p.	1.3
P_4 , tr.	1.2
Length M_T - M_3	5.8	5.7	...	5.4	5.8
M_T , a.-p.	2.2	2.5	2.2	2.4	...
M_T , tr.	1.4	1.4	1.5	1.5	...
M_2 , a.-p.	2.1	1.9	1.9	1.8	2.0
M_2 , tr.	1.2	1.3	1.4	1.4	1.4
M_3 , a.-p.	1.6	1.6	...	1.5	1.8
M_3 , tr.	1.1	1.1	...	1.1	1.2
Depth of ramus under M_T	2.4	2.5	2.5	2.2	2.5

* Measurements from Scott.

† The lower figure is perhaps due to less precise methods of measuring.

‡ 2.5 under M_2 .

The measurements given for *D. crassigenis* by Cope in 1874 do not agree with those given by him in 1884; consequently neither set is included here.

NOTE ON MYSTIPTERUS VESPERTILIO HALL

This form, based on a fragment of the left mandible with M_3 , from the Esmeralda, lower Pliocene, of Nevada, was described by Hall (1930) as a bat and referred to the Vespertilionidae. He compared the specimen with *Miniopterus* and noted the following distinctions, regarding them as of generic significance only: (1) paraconid-protoconid blade distinctly notched and with strong cingulum at its base; (2) each of the five principal cusps present but without accessory cusps; (3) trigonid longer than talonid, even on medial side; (4) talonid basined; (5) masseteric fossa deep. All of these characters, however, are typically soricid and appear to us, therefore, to be of ordinal significance.

Other important differences from *Miniopterus* and resemblances to the Soricidae are (a) masseteric fossa extending downward much nearer the ventral margin of the jaw; (b) that part of the jaw behind the anterior margin of the masseteric fossa notably less upturned; (c) talonid relatively shorter; (d) ramus relatively heavier. From the evidence available we believe that *Mystipterus vespertilio* must be transferred from the Vespertilionidae to the Soricidae.

Erinaceidae Bonaparte

The genus described below has not hitherto been placed in this family. The reasons for the assignment are given in the discussion of affinities on p. 267.

Metacodon Clark

Metacodon Clark 1936, in Scott and Jepsen, Trans. Amer. Phil. Soc., N. S., 28, p. 22.

Genotype.—*Metacodon magnus* Clark 1936.

Distribution.—Lower Oligocene, Chadron beds, South Dakota; Middle Oligocene, Lower Brulé beds, Nebraska and Colorado.

Emended diagnosis.— $I_3^?$, $C_1^?$, $P_4^?$, M_3^3 . P^4 submolariform with parametacone, strong parastyle, metastyle crest. Upper molars narrow transversely, protoconules absent, metaconules absent or very small, external shelves wide with stylar cusps varyingly developed, parastyles strong, metastyle crest on M^{1-2} , hypocone of M^3 small. Lower C small, erect. P_1 two rooted; P_3 small in comparison with P_{2-4} ; P_4 submolariform with metaconid not completely separated from, directly lingual to, and lower than protoconid; anterior cusp and talonid small, low. Trigonids of lower molars much higher than talonids, base of paraconid situated high on talonid. Horizontal ramus slender, shallow.

Metacodon magnus Clark

M. magnus Clark 1936, in Scott and Jepsen, Trans. Amer. Phil. Soc., N. S., 28, p. 23, pl. 2, figs. 5, 5a.

Holotype.—Princeton Univ. Mus. No. 13835, portion of right mandible with P_4 – M_3 .

Horizon.—Chadron beds. Big Corral Draw, South Dakota.

Diagnosis.—Larger than *M. mellingeri*, M_{1-3} 6.0 mm.¹ Upper molars relatively wider transversely, hypocone more prominent. P_4 with metaconid larger and better separated from protoconid.

¹ We are indebted to Dr. Clark for supplying this measurement from his MS.

M_3 relatively larger and with narrower talonid, hypoconulid forming sharp postero-internal angle on talonid basin rim, rim continuous between entoconid and metaconid.

Remarks.—Knowledge of the upper molars of *M. mellingeri* permitted identification of upper molars of *M. magnus* among miscellaneous lots of Chadron specimens in the Princeton University Museum. Comparisons between the two species in the postdental region of the mandible showed that the character of *M. magnus* upon which Clark chiefly relied in erecting the genus—the reduction of the angle and lowering of the condyle—cannot be regarded as established. The holotype was found in fragments, and the contacts in the posterior region, although apparently good, were found on close re-examination to be inexact. This matter will be discussed by Dr. Clark in his forthcoming paper on the Chadron beds. The genus is fully validated, however, by the new material described here.

***Metacodon mellingeri* sp. nov. (figs. 66, 67, 69–72)**

Holotype.—F.M. No. P15321, incomplete right mandible with P_1 , P_4 , M_{1-3} , and alveoli of P_{2-3} .

Horizon and locality.—Lower Brulé beds. Sec. 12, R. 65 W., T. 11 N., three miles N.W. of Gault Schoolhouse, Weld County, Colorado. Collected by Mr. James Mellinger, in whose honor the specific name is given.

Paratypes.—F.M. No. P15322, incomplete left mandibular ramus with P_{3-4} and alveoli of I_1 – P_2 ; F.M. No. 15323, portion of right mandibular ramus with C, P_{1-2} ; Univ. Chicago No. 1555, left maxillary with P^4 – M^3 ; Univ. Chicago No. 1556, M^{1-2} and portion of right mandible with M_{2-3} ; Univ. Chicago No. 1557, portion of left mandible with P_4 – M_3 ; Univ. Chicago No. 1558, portion of right mandible with P_4 – M_2 ; Univ. Chicago No. 1559, left mandible with P_4 – M_2 ; Univ. Chicago No. 1560, portion of left maxillary with P^4 – M^2 . The Field Museum paratypes were collected by Mr. Mellinger at the same horizon and locality as the holotype. Univ. Chicago Nos. 1555, 1556, 1557, 1558, and 1560 were collected by McGrew from the lower Brulé (Middle "*Oreodon*" level), twelve miles N.N.W. of Crawford, Dawes County, Nebraska; No. 1559, from the same horizon eight miles N.E. of Harrison, Sioux County, Nebraska.

Diagnosis.—Smaller than *M. magnus*, M_{1-3} 4.9–5.3 mm. Upper molars relatively narrower, hypocone slightly less developed. P_4 with metaconid only slightly separated, anterior cusp lower and smaller. M_3 relatively smaller with narrower talonid, hypoconulid

projecting posteriorly as on M_{1-2} , basin rim not continuous between entoconid and metaconid.

Description.—In strong contrast to the leptictids, P^4 is not molariform. The parametacone of P^4 is large and high, wider trans-

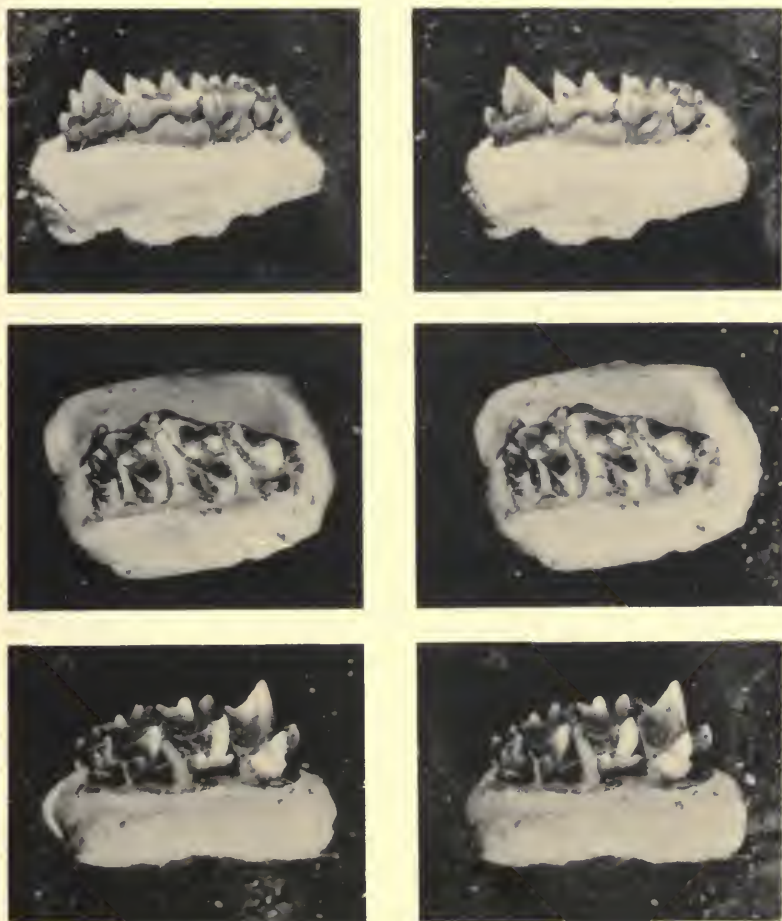


FIG. 66. *Metacodon mellingeri* sp. nov. Univ. Chicago No. 1555. Paratype. Right P^4 — M^2 in maxilla fragment; external, crown, and internal views. $\times 5$

versely and higher than either the paracone or metacone of M^1 . The metastyle crest is well developed. The protocone is prominent and sharp, but is smaller than that of M^{1-2} ; it is somewhat inclined anteriorly. A poorly defined ridge runs from its apex to the base

of the antero-internal slope of the parametacone. The parastyle is large, cuspidate, directly anterior to and well separated from the parametacone, and strongly protruding. It forms a right angle with the ridge running anteriorly from the protocone. The metastyle is a stout cusp inclined posteriorly. It bears two small stylar cuspules arranged antero-posteriorly on its anterior slope, the posterior being the larger of the two. The external cingulum connects the parastyle and metastyle, but is very weak external to the parametacone. The anterior cingulum is merely a slight swelling at

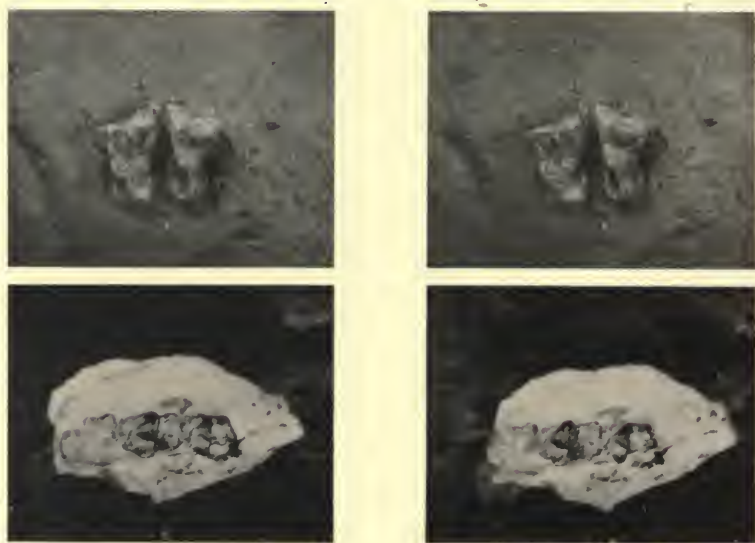


FIG. 67. *Metacodon mellingeri* sp. nov. Univ. Chicago No. 1556. Paratype. Left M^{1-2} , portion of right ramus with M_{2-3} ; crown views. $\times 5$

the base of the anterior slope of the protocone. The posterior cingulum is more extensive than on the molars, extending from the metastyle inward to the postero-internal corner of the protocone, where it thickens to a slight hypocone.

On M^1 the paracone and metacone are subequal and lower than the parametacone of P^4 . They are fairly close together, much as in *Tupaiodon*, and have a short thick ridge connecting their bases. The protocone is large, high and notably inclined anteriorly, this inclination imparting a somewhat twisted appearance to the tooth. Ridges from the protocone apex run externally around the bases of the para- and metacone to the para- and metastyle, the anterior

ridge being considerably the higher of the two. In contrast to *Tupaiodon* neither ridge shows any proto- or metaconule thickening. To judge from P^4 , it would appear that the developing posterior ridge may have captured the external portion of the posterior cingulum. The parastyle is large, low, and blunt. It is strongly protruding, but not so much as that of P^4 , and is situated anterior and slightly external to the paracone. The parastyle bears on its posterior slope a stylar cuspule, which is demarcated from it externally by a small shallow groove. The metastyle projects externally to a much greater degree than the parastyle. It is rather wider transversely than that of P^4 , and lacks stylar cuspules. The metastyle crest is prominent, a decidedly erinaceid character. The external cingulum forms a moderate shelf which turns rather sharply

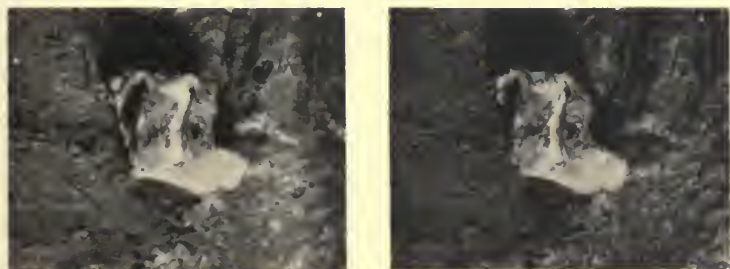


FIG. 68. ?*Metacodon* sp. Univ. Chicago No. 1561. Left M^{1-2} in maxilla fragment; crown view. $\times 5$

outward and backward around the metastyle. The anterior cingulum is similar to that of *Tupaiodon*, extending internally to the antero-internal slope of the protocone. The posterior cingulum also resembles that of the Mongolian form, but the hypocone is not so robust.

The paracone and metacone of M^2 differ from those of M^1 in that the notch between them is somewhat deeper, and the metacone is postero-internal to the paracone. The protocone is less inclined anteriorly, and its posterior ridge is not so robust. The very large parastyle is antero-external to the paracone. As in most erinaceids, it is larger and more salient than the metastyle on this tooth, the reverse of the conditions seen on M^1 . Its stylar cuspule is larger than that of M^1 and is demarcated externally by a posterior groove in addition to the median one. The metastyle crest is shorter and notably lower than that on M^1 . The external shelf is wider than on the preceding tooth and has a deep median cleft. The anterior

cingulum extends around to the lingual slope of the protocone, just meeting the posterior cingulum. The latter is similar to that on M^1 , but the hypocone is slightly smaller.

The paracone of M^3 is slightly higher than the metacone, and rather more antero-external to it than on M^2 . The protocone is relatively higher than on M^{1-2} and actually higher than the para-

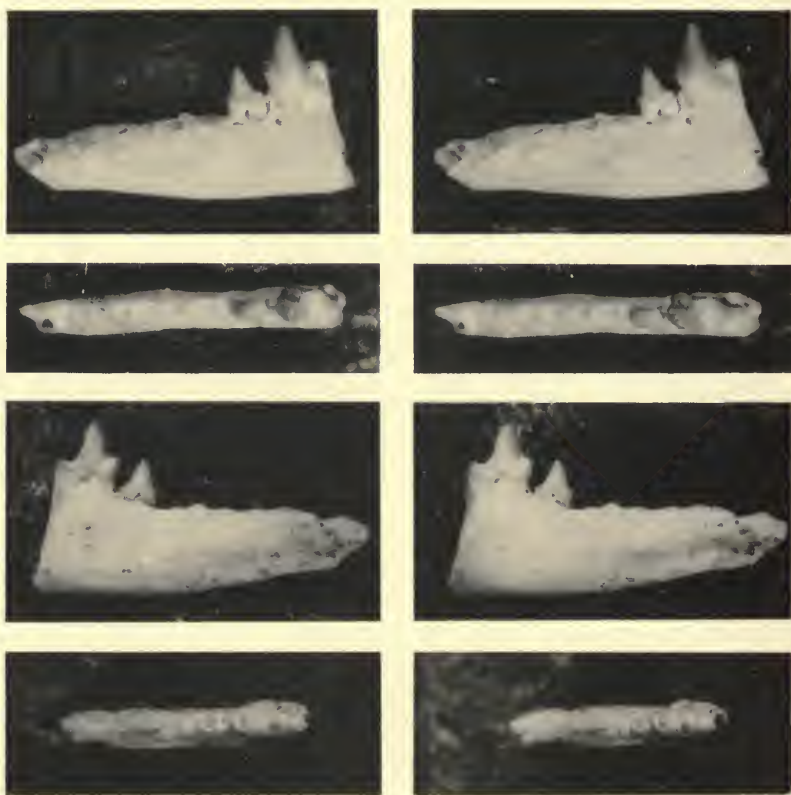


FIG. 69. *Metacodon mellingeri* sp. nov. F. M. No. P15322. Paratype. Portion of left ramus with symphysis, P_3-4 ; external, crown, internal, and anterior views. $\times 5$

cone. The posterior ridge is higher than on the preceding teeth enclosing a moderately deep central basin. The parastyle is extremely large and projects externally to a marked degree. Its stylar cusp is very slight. The metastyle is greatly reduced and the crest is lacking. The external cingulum forms a much smaller shelf than on the preceding molars. The hypocone is merely a slight enlargement of the internal extremity of the posterior cingulum.

The description given above has been taken from Univ. Chicago No. 1555, which is by far the best upper dentition so far obtained. The few differences exhibited by other specimens may be briefly noted. On Univ. Chicago No. 1556, and on this specimen only, there occurs a small ridge running directly inward from the base of the metacone to the ridge extending posteriorly from the protocone apex. This ridge is important since it appears to represent the metaconule (fig. 67). A specimen collected in the lower Brulé north-east of Harrison and consisting of M^{2-3} in a maxilla fragment (Univ.

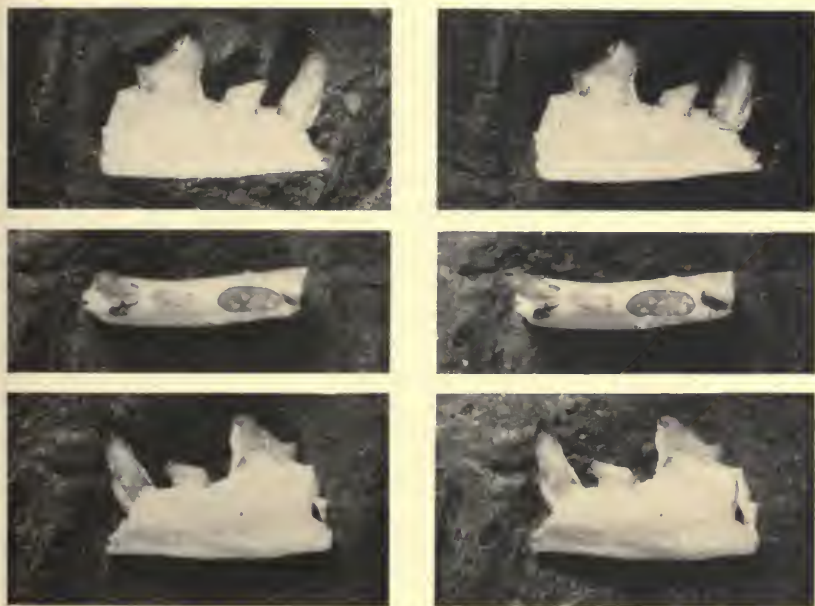


FIG. 70. *Metacodon mellingeri* sp. nov. F. M. No. P15323. Paratype. Fragment of right ramus with portion of symphysis, canine, P_{1-2} ; external, crown, and internal views. $\times 5$

Chicago No. 1561) differs in several characters from the remainder of the material and is probably not referable to *M. mellingeri* and possibly not to *Metacodon* (fig. 68). Both teeth are notably narrower than in the paratypes, and have the anterior cingulum somewhat thickened internally. The metastyle of M^2 is external rather than postero-external to the metacone, and the external cleft between the para- and metastyle is much deeper. On M^3 the hypocone is prominent, and extends posteriorly to a slight extent. When more material is obtained, this specimen may prove to represent a distinct genus.

The lower incisors are not preserved. The alveoli show that they were subequal, moderately procumbent, and arranged in a nearly antero-posterior row. The roots were long. The only canine preserved is considerably worn. It is a small, blunt, erect, single rooted tooth, apparently lower than P_4 and the molars. The labial side is convex, the lingual slightly fluted anteriorly. The transverse diameter is slight. The single rooted canine of this form and of *Tupaiaodon morrisi* indicate that Leche may have been incorrect in his belief that double-rooted canines were primitive for the family.

All the premolars are double-rooted. P_1 is notably procumbent and consists of a robust blunt cusp and a minute posterior cuspule. P_2 is a much larger tooth than either P_1 or P_3 . It is erect and long with a large cusp at the anterior extremity and with a small heel. P_3 is very small in comparison with P_4 ; it has a stout central cusp, a small anterior cuspule, and a slight heel. P_4 is as high as, or in some cases even slightly higher, than the molars. The metaconid is partially separated from the protoconid, but not to such an extent as in *M. magnus*, and is definitely the lower of the two cusps. A variable antero-external cingulum is present which extends upward to the low, small anterior cusp. The heel is fairly well developed and somewhat excavated transversely; it is rather high on the lingual side and slopes down toward the labial, forming a semi-trenchant heel.

The first and second lower molars are nearly subequal, M_2 being almost imperceptibly the larger of the two; M_3 is somewhat smaller. The trigonid and talonid of M_1 are approximately equal in width, but the trigonid is much higher and slightly longer. The protoconid forms a sharp external angle, and is somewhat larger and higher than the metaconid. The paraconid is lower than the metaconid and is situated in front of and close to it. The bases of these cusps are high on the trigonid and consequently the cusps themselves become obliterated by moderate wear. The antero-external cingulum is well developed but does not reach the paraconid. The talonid cusps together form an elevated posterior rim, the hypoconid being postero-external and angulate externally, the entoconid postero-internal. The hypoconulid is in the middle of the posterior rim and projects posteriorly to a moderate degree, less, however, than in *Ictops*. Ridges from the apices of the entoconid and hypoconid slope down anteriorly to the base of the trigonid. The talonid basin is well defined and quite deep.

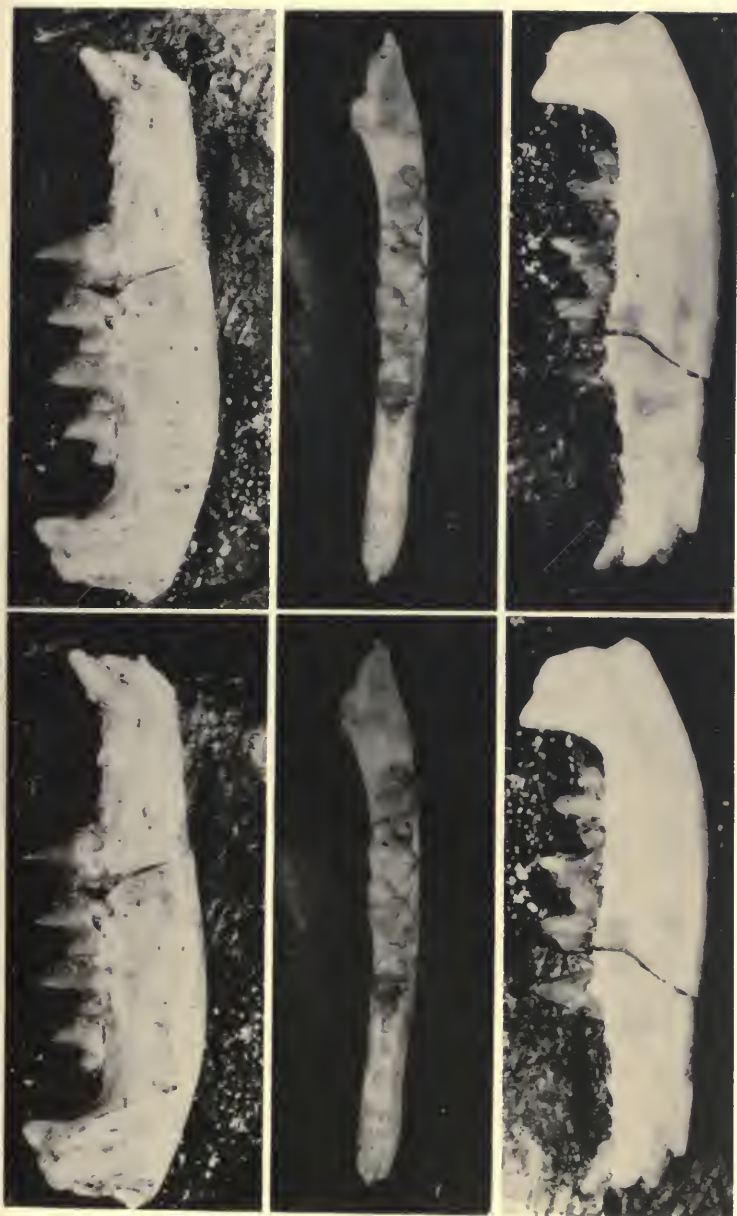


FIG. 71. *Metacodon mellingeri* sp. nov. F. M. No. P15321. Holotype. Incomplete right mandible with P_1 , P_4-M_3 ; external, crown, and internal views. $\times 5$

On $M_{\overline{2}}$ the trigonid is wider transversely and narrower antero-posteriorly, with the paraconid even closer to the metaconid than on $M_{\overline{1}}$. The hypoconulid is rather more internal in position, and more closely connected to the entoconid. The latter cusp is smaller and more anterior in position. The talonid of $M_{\overline{3}}$ is relatively narrower than on $M_{\overline{1}-\overline{2}}$; the hypoconid is not as angulate externally, and the entoconid is notably reduced in size.

The horizontal ramus of the mandible is shallow, slender, and long; the ventral border curves upward beneath the ascending ramus. The ligamentous symphysis extends posteriorly to a point

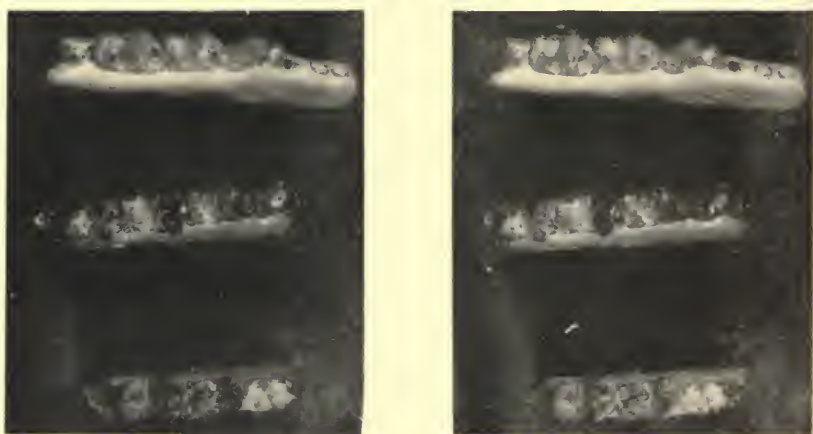


FIG. 72. *Metacodon mellingeri* sp. nov. Univ. Chicago No. 1559, portion of left ramus with P_4-M_3 . U. C. 1557, portion of left ramus with P_4-M_3 . U. C. 1558, portion of right ramus with P_4-M_2 . Crown views of paratypes. $\times 5$

beneath the anterior half of $P_{\overline{2}}$. The ascending ramus arises well behind $M_{\overline{3}}$ and is moderately heavy. The deep masseteric fossa is sharply defined anteriorly by a strong ascending ridge. The anterior mental foramen is either beneath $P_{\overline{1}}$ (P15323) or beneath the anterior root of $P_{\overline{2}}$ (P15321, P15322), the posterior beneath the posterior root of $P_{\overline{3}}$.

Affinities.—Clark (*in* Scott and Jepsen 1936, p. 22) referred *Metacodon* to the Leptictidae, and regarded it as a probable descendant of *Leptacodon*. This reference was fully justified by the material at his disposal, since the lower molars are very similar to those of typical leptictids. The new material described here shows, however, that the genus can hardly be placed in that family. The

undivided parametacone of P^4 , the wide external shelves, strong styles, metastyle crests, and more centrally placed paracone and metacone of the upper molars sharply distinguish *Metacodon* from the Leptictidae. Members of this family had already acquired the molariform P^4 in the upper Cretaceous (e.g. *Gypsonictops*). The holotype of *Leptacodon tener*, the genotypic species, is typically leptictid. The genus therefore cannot be considered as ancestral, or even closely related, to the form under consideration. There is a possibility that some of the species that have been placed in *Leptacodon* may not belong in the genus, but this question is outside the scope of the present paper.

Since *Metacodon* is excluded from the Leptictidae, its family position remains to be determined. In all the characters in which the genus differs from leptictids, it shows a decidedly close resemblance to the Erinaceidae. The various genera of this family, living and extinct, appear to be fundamentally similar in dental characters to the form under discussion. The likeness of P^4 appears to be especially significant. The upper molars of the recent genera are wider transversely, the hypocones are larger, and the external cingula and metastyle crests are less prominent. Such differences as these, however, are to be expected between an Oligocene genus and existing forms. *Tupaiaodon*, of the Oligocene of Mongolia, tentatively regarded as a tupaiaid by Matthew and Granger (1924, p. 1, fig. 1), but transferred to the Erinaceidae by Simpson (1931, p. 12), and *Proterixoides* (Stock 1935) of the upper Eocene of California are partly intermediate between *Metacodon* and the more advanced members of the family, particularly as regards the transverse diameter of the upper molars. The lower molars of *Metacodon* differ from those of most erinaceids in having higher and more antero-posteriorly compressed trigonids, and distinct hypoconulids; characters which approach those of the Leptictidae. Although in part primitive, these differences may, and probably do, indicate that the genus is a representative of a somewhat aberrant side branch of the Erinaceidae,¹ but we do not believe that they are of sufficient importance to warrant exclusion from the family. The new genus *Ankylodon* described below, appears to be structurally intermediate in lower molar pattern between *Metacodon* and the more typical erinaceids. ?*Tupaiaodon minutus* has a very distinct hypoconulid on M_3 (fig. 73), as has *Proterixoides davisii* (Stock 1935, pl. 1, fig. 2),

¹ The occurrence of *Proterix*, a more typical member of the family, in the Brulé tends to support this view.

and we have detected a small hypoconulid on M_{T-2} of a specimen of *Hemiechinus* in the Field Museum collection (No. 35811).

Metacodon shows similarities to the tupaiids, but the resemblances are not as close to this family as to the erinaceids. The upper molars are rather like those of early pantolestids, e.g. *Bes-soecetor*, but the very different P_4 seem definitely to preclude close relationship.

The position of *Metacodon* within the Erinaceidae is uncertain. The living members of the family are customarily divided into two subfamilies, the Erinaceinae and the Echinisoricinae.¹ The former is certainly a natural group, but the latter may include more than one stock. In any event, *Metacodon* appears to stand in about the same structural relation to the living echinosoricines as they in turn

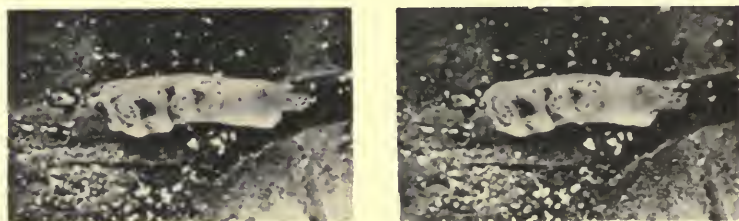


FIG. 73. ?*Tupaiodon minutus* Matthew and Granger. F. M. No. P14124. Portion of left ramus with M_{2-3} ; crown view. $\times 5$

stand to the erinaceines. Further than this it is impossible to go at present.

Entomolestes, from the middle Eocene Bridger and lower Eocene Gray Bull beds, was provisionally placed by Matthew (1909b, pp. 541-542, pl. 50, fig. 2) in the Talpidae, although he stressed its resemblances to the Tupaiidae, and later (1918, p. 597) referred it tentatively to this family. Simpson at first referred it to the Adapisoricidae (1928, pp. 5-6), but later (1931, p. 17) considered it to be an erinaceoid and possibly a leptictid. We believe that the non-molariform P_4 indicates that it should be referred provisionally to the Erinaceidae. One rooted P_{2-3} occur in the living genus *Hylomys*. The heel of P_4 is very similar to that of *Metacodon*, and M_{2-3} are close to those of ?*Tupaiodon minutus* (fig. 73).

¹ Cabrera (1925, p. 58) has shown that the widely used named *Gymnura* Lesson is unfortunately preoccupied and must be replaced by *Echinorex* Blainville 1838.

MEASUREMENTS IN MILLIMETERS

	U. C. 1555	U. C. 1556	Holotype P15321	P15322	P15323	U. C. 1557	U. C. 1558	U. C. 1559
P_1^1 , a.-p.*	2.0
P_1^1 tr.*	1.0
Length M_1^1 - a	3.8
M_1^1 , a.-p.	1.2	1.2
M_1^1 tr.	2.3	2.3
M_2^2 , a.-p.	1.0	1.1
M_2^2 tr.	2.3	2.3
M_3^3 , a.-p.	.9
M_3^3 tr.	1.9
C , a.-p.	1.0
C , tr.4
Length P_1 - M_3	10.9
Length P_1 - P_4	6.1
P_1 , a.-p.	1.2	...	1.0
P_1 tr.54
P_2 , a.-p.	1.8
P_2 tr.7
P_3 , a.-p.	1.1
P_3 tr.6
P_4 , a.-p.	1.6	1.8	...	1.6	...	1.7
P_4 tr.9	.988
Length M_1 - P_3	4.9	5.3
M_1 , a.-p.	1.8	1.8	1.7	1.8
M_1 tr.	1.1	1.0	1.0	1.0
M_2 , a.-p.	...	1.8	1.9	1.9	1.9	1.9
M_2 tr.	...	1.1	1.2	1.2	1.2	1.2
M_3 , a.-p.	...	1.4	1.5	1.6
M_3 tr.8	.9	1.0
Depth of ramus under P_1	2.1	1.8	1.9
Depth of ramus under M_2	2.7	2.5	3.0

* The antero-posterior diameters of the upper cheek teeth have been measured across the bases of the lingual slopes of the paracones and metacones, the transverse across the centers of the teeth.

Ankylodon¹ gen. nov.

Genotype.—*Ankylodon annectens* sp. nov.

Distribution.—Middle Oligocene, Lower Brulé beds, Colorado.

Diagnosis.— P_4 submolariform, protoconid and metaconid curving backward, metaconid lower than protoconid. M_{1-2} with trigonids extending forward in advance of the anterior root and with a moderate backward curvature; trigonids lower, and teeth as a whole broader than in *Metacodon*; external sides of protoconids and hypoconids strongly convex; paraconids notably reduced; hypoconulids distinct, connected with hypoconids and entoconids.

Ankylodon annectens² sp. nov. (fig. 74)

Holotype.—F.M. No. P15326, portion of left ramus with P_4 - M_2 .

¹ In allusion to the curved trigonids.

² In allusion to its structurally intermediate position between *Metacodon* and more typical erinaceids in lower molar structure.

Horizon and Locality.—Lower Brulé beds. Sec. 12, R. 65 W., T. 11 N., three miles N.W. of Gault Schoolhouse, Weld County, Colorado. Collected by Mr. James Mellinger.

Diagnosis.—As for the genus, for measurements see below.

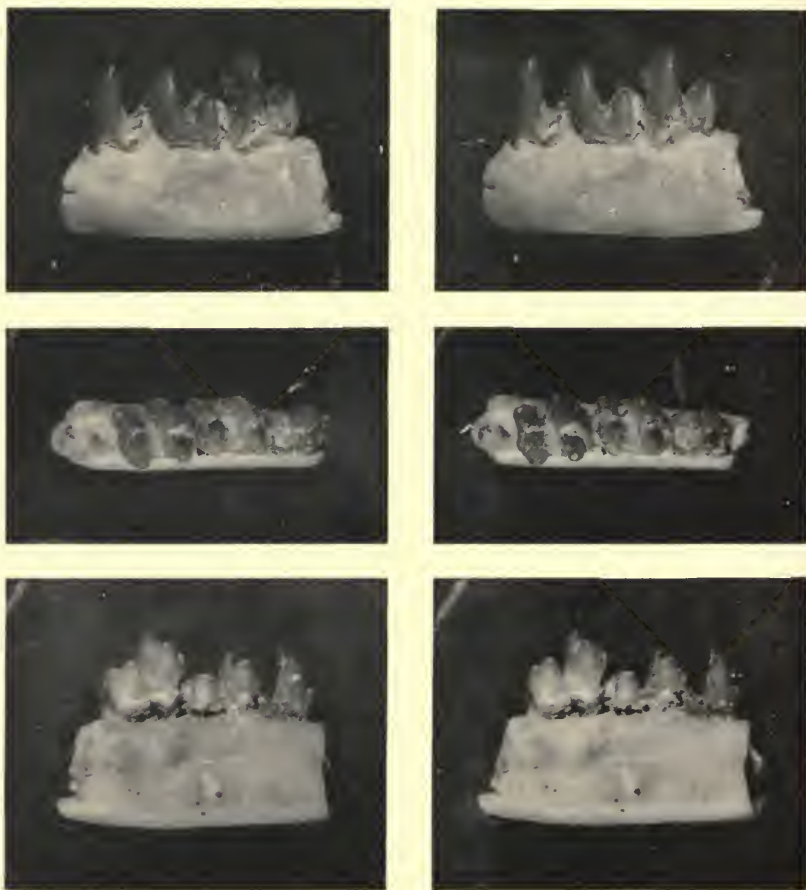


FIG. 74. *Ankylodon annectens* gen. et sp. nov. F. M. No. P15326. Holotype. Portion of left ramus with P_4 – M_2 ; external, crown, and internal views. $\times 5$

Description.—The anterior cusp of P_4 forms a low shelf across the front of the tooth. The metaconid is well separated from the protoconid, rather more so than in *Metacodon mellingeri*. The heel is very similar to that of *Metacodon*, but is definitely lower on the tooth. Cingula are not developed. M_{1-2} are almost identical in

structure; both extend anteriorly, and display the same degree of backward curvature of the trigonid and strong convexity of the labial faces of the proto- and hypoconids. The trigonids are narrow antero-posteriorly; the paraconids are reduced to mere ridges. Weak antero-external cingula are present. The protoconids are higher than the metaconids. The entoconids are larger and rather higher than the hypoconids. As in *Metacodon*, the three talonid cusps form an elevated posterior rim. The hypoconulids are more nearly in transverse alignment with the hypo- and entoconids. The trigonids and talonids are sharply separated by a deep transverse groove. The small portion of the ramus present is nearly uniform in depth throughout. The small posterior mental foramen is anterior to P_4 , presumably beneath the posterior root of P_3 as in *Metacodon*.

Ankylodon is definitely erinaceid in structure. Its various points of similarity to *Metacodon* therefore strengthen the reference of the latter genus to the Erinaceidae, as noted above.

MEASUREMENTS IN MILLIMETERS

P_4 a.-p.....	1.6
P_4 tr.....	1.2
M_1 a.-p.....	1.8
M_1 tr.....	1.4
M_2 a.-p.....	2.0
M_2 tr.....	1.6
Depth of ramus under M_1	2.8

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